remataceae, but excludes Verbenoideae and the segregate families Stilbaceae, Nesogenaceae, and Cyclocheilaceae; in the latter four groups, the ovules are borne directly on the carpel margins (Junell, 1934). Sequence data for the *rbc*L gene (Olmstead et al., in press) also suggest that subfamily Viticoideae is more closely related to the Labiatae than is subfamily Verbenoideae (no members of Chloanthoideae, Caryopteridoideae, or the segregate families have yet been included in Olmstead's study).

Subfamily Verbenoideae and the other outlying groups of Verbenaceae sensu lato, for which data collection is still very incomplete, will be included in a subsequent analysis. However, they have been used here in a limited way as outgroups (discussed below). *Amasonia* and *Monochilus*, usually assigned to subfamily Verbenoideae as tribe Monochileae (e.g., Briquet, 1895; Moldenke, 1971), have been included here because their gynoecial morphology (Junell, 1934), pollen morphology (Raj, 1983, 1987), and leaf epidermal anatomy (Cantino, 1990a) strongly suggest that their true affinities lie with the Viticoideae.

In the Labiatae, all genera of Ajugeae and Prostanthereae, as well as 16 other genera, are included in the analysis. The two large clades of gynobasic-styled Labiatae, subfamily Nepetoideae sensu Erdtman (1945) and subfamily Lamioideae sensu Wunderlich (1967) (= tribe Lamieae sensu Abu-Asab & Cantino (1987)), are represented by only a few exemplar genera each. The monophyly of both groups is well supported (Cantino & Sanders, 1986; Abu-Asab & Cantino, 1987). An unfortunate omission from the study group is *Wenchengia* C. Y. Wu & S. Chow. Its shallowly lobed ovary (Wu & Chow, 1965) is reminiscent of tribes Ajugeae and Prostanthereae, but its alternate leaves and unique fruit structure (a schizocarp with four mericarps attached to carpophores) led Wu & Chow (1965) to segregate it as a monotypic subfamily Wenchengioideae. An effort will be made to borrow herbarium material of this rare and possibly primitive Chinese taxon so that it may be included in a future analysis.

Although most of the 106 unit taxa (OTUs) are genera (Table 2), a few genera whose monophyly is seriously in question have been divided into less inclusive units. In the case of *Pityrodia*, for example, a paraphyletic genus of 41 species, 10 exemplar species were used as separate OTUs.

SOURCES OF DATA

Seventy-one of the 85 characters employed in the analysis (Table 3) concern floral, fruit, or veg-

etative morphology. The remaining characters are embryological (3), palynological (5), phytochemical (1), or concern leaf epidermal anatomy (5). The data for embryological characters 68 and 79 were obtained from Junell (1934), Misra (1939), Martin (1946), Pal (1951), Wunderlich (1967), and my own observations on character 79. Information on pollen morphology was obtained from Cantino (1982a), Raj (1983, 1987), Raj & Grafström (1984), Abu-Asab & Cantino (1989), Abu-Asab (1990 and unpublished SEM photos), and S. Wagstaff (unpublished SEM photos of Nepetoideae). The data for the single phytochemical character were obtained from Hagemann et al. (1967), and unpublished information was supplied by Robert Kleiman. The data for characters 2–6 derive from an ongoing survey of leaf epidermal anatomy in the Lamiales (Abu-Asab & Cantino, 1987; Cantino, 1990a, and unpublished data).

The scoring of the 71 morphological characters was based largely on my firsthand observations. Herbarium specimens provided the bulk of the morphological data, but living plants and liquid-preserved flowers and fruits were examined whenever possible. The extensive living collections of Labiatae and Verbenaceae at the Royal Botanic Gardens, Kew, and those maintained by me at Ohio University were helpful in understanding the variation in floral and fruit morphology. Descriptions in monographs and floras were consulted in order to reduce the likelihood of errors and to develop a better understanding of intra-OTU variation, but this study has not relied heavily on the literature for the morphological data.

Characters 50 and 78 have been included with a bit of trepidation because their states are frequently difficult to distinguish in herbarium material. Their low consistency indices may be due in part to incorrect observations rather than true homoplasy. Clades supported principally or entirely by these characters cannot be accepted with much confidence. Other characters (particularly 68 and 85) are problematical because of small sample size (i.e., only a few species have been examined per OTU). They do not suffer from excessive homoplasy, but further study may reveal more intra-OTU variation than is recognized at present.

An effort has been made to code the characters so as to maximize their independence, but it has not been possible to eliminate character correlation entirely. Non-independence of characters can result in unintentional weighting (see Affinities of *Physopsis* and *Faradaya* for an example). Most multistate characters were treated as unordered (i.e., a change from any state to any other adds a single step to the tree), but nine characters (spec-

TABLE 2. Unit taxa (OTUs) employed in the cladistic analysis. Names at left are OTU labels in Figures 1–4. Parenthetical acronyms indicate infrafamilial taxa to which the OTU is generally assigned (see Table 1).

ACRYMIA = *Acrymia* Prain (AJ)
AEGIPHIL = *Aegiphila* Jacq. (CAL)
AJUGA = *Ajuga* L. (AJ)
AMASONIA = *Amasonia* L.f. (MO)
AMETHYST = *Amethystea* L. (AJ)
ANISOMEL = *Anisomeles* R. Br. (GL)
CALLICAR = *Callicarpa* L. (including *Geunsia* Blume) (CAL)
CARYBICO = *Caryopteris bicolor* (Hardw.) Mabb. (CAR)
CARYCARY = *Caryopteris* Bunge sect. *Caryopteris* (CAR)
CARYDIVA = *Caryopteris divaricata* (Siebold & Zucc.) Maxim. (CAR)
CARYGRAT = *Caryopteris grata* Benth. & Hook. f. (CAR)
CARYNEPA = *Caryopteris nepalensis* Mold. (CAR)
CARYNEPE = *Caryopteris nepetifolia* (Benth.) Maxim. (CAR)
CARYPANI = *Caryopteris paniculata* Clarke (CAR)
CARYSICC = *Caryopteris siccanea* W. W. Smith (CAR) (including *Cardioteucris* C. Y. Wu; see Cantino
           [1991])
CARYTERN = *Caryopteris terniflora* Maxim. (CAR)
CHLOANTH = *Chloanthes* R. Br. (CH)
CLERCYCL = *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke (except sect. *Pleurocymosa*) (CL)
CLERKONO = *Clerodendrum* L. subg. *Clerodendrum* sect. *Konocalyx* B. Thomas (CL)
CLERMINA = *Clerodendrum minahassae* Teijsm. & Binnend. (CL)
CLERNUDI = *Clerodendrum nudiflorum* Mold. (CL)
CLERODEN = *Clerodendrum* L. (all species not included in other OTUs) (CL)
CLERPLEU = *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke sect. *Pleurocymosa* B. Thomas (CL)
CLERVOLK = *Clerodendrum* L. subg. *Volkameria* (L.) Briq. (CL)
COLEBROO = *Colebrookea* Smith (GL)
CORNUTIA = *Cornutia* L. (VI)
CYANOSTE = *Cyanostegia* Turcz. (CH)
CYMARIA = *Cymaria* Benth. (AJ)
DICRASTY = *Dicrastylis* J. L. Drumm. ex Harvey (PH)
EICHLERA = *Eichlerago* Carrick (PR)
FARADAYA = *Faradaya* F. Muell. (CL)
GALEOPSI = *Galeopsis* L. (GL)
GARRETTI = *Garrettia* Fletcher (VI)
GLECHOMA = *Glechoma* L. (NE)
GLOSSOCA = *Glossocarya* Wallich ex Griffith (CAR)
GMELINA = *Gmelina* L. (VI)
HARLANLE = *Harlanlewisia* Epling (SC)
HEMIANDR = *Hemiandra* R. Br. (PR)
HEMIGENI = *Hemigenia* R. Br. (PR)
HEMIPHOR = *Hemiphora* (F. Muell.) F. Muell. (CH)
HOLMSKIO = *Holmskioldia* Retz. sensu Fernandes (1985) (CL)
HOLOCHEI = *Holocheila* (Kudo) S. Chow (AJ)
HOSEA = *Hosea* Ridley (CL)
HUXLEYA = *Huxleya* Ewart (CL)
HYMENOPY = *Hymenopyramus* Wallich ex Griffith (CAR)
KALAHARI = *Kalaharia* Baillon (CL)
KAROMIA = *Karomia* Dop sensu Fernandes (1985) (CL)
LACHNOST = *Lachnostachys* Hook. (PH)
LAMIUM = *Lamium* L. (GL)
MALLOPHO = *Mallophora* Endl. (PH)
MELISSA = *Melissa* L. (NE)
MICROCOR = *Microcorys* R. Br. (PR)
MOLUCCEL = *Moluccella* L. (GL)
MONARDA = *Monarda* L. (NE)
MONOCHIL = *Monochilus* Fischer & C. Meyer (MO)

TABLE 2.   Continued.

NEORAPIN = *Neorapinia* Mold. (TEC)
NEWCASTE = *Newcastelia* F. Muell. (PH)
ONCINOCA = *Oncinocalyx* F. Muell. (CL)
OXERA = *Oxera* Labill. (CL)
PARAVITE = *Paravitex* Fletcher (VI)
PERILOMI = *Perilomia* Kunth (*Scutellaria* L. sects. *Perilomia* (Kunth) Epling and *Perilomioideae* (Benth.)
  Epling) (SC)
PERONEMA = *Peronema* Jack (CAR)
PETITIA = *Petitia* Jacq. (TEC)
PETRAEOV = *Petraeovitex* Oliver (CAR)
PHYSOPSI = *Physopsis* Turcz. (PH)
PHYSOSTE = *Physostegia* Benth. (GL)
PITYANGU = *Pityrodia angustisepala* Munir (CH)
PITYBART = *Pityrodia bartlingii* (Lehm.) Benth. (CH)
PITYBYRN = *Pityrodia byrnesii* Munir (CH)
PITYDILA = *Pityrodia dilatata* (F. Muell.) Benth. (CH)
PITYHALG = *Pityrodia halganiacea* (F. Muell.) E. Pritzel (CH)
PITYLOXO = *Pityrodia loxocarpa* (F. Muell.) Druce (CH)
PITYOLDF = *Pityrodia oldfieldii* (F. Muell.) Benth. (CH)
PITYPANI = *Pityrodia paniculata* (F. Muell.) Benth. (CH)
PITYSALV = *Pityrodia salvifolia* R. Br. (CH)
PITYUNCI = *Pityrodia uncinata* (Turcz.) Benth. (CH)
POGOSTEM = *Pogostemon* Desf. (including *Eusteralis* Raf.) (GL)
PRASIUM = *Prasium* L. (GL)
PREMNA = *Premna* L. (VI)
PROSKLAN = *Prostanthera* Labill. sect. *Klanderia* (F. Muell.) Benth. (PR)
PROSPROS = *Prostanthera* Labill. sect. *Prostanthera* (PR)
PRUNELLA = *Prunella* L. (NE)
PSEUDOCA = *Pseudocarpidium* Millsp. (VI)
PYGMAEOP = *Pygmaeopremna* Merr. (VI)
RENSCHIA = *Renschia* Vatke (AJ)
RUBITEUC = *Rubiteucris* Kudo (AJ)
SALAZARI = *Salazaria* Torrey (SC)
SCHNABEL = *Schnabelia* Hand.-Mazz. (AJ)
SCUTELLA = *Scutellaria* L. (excluding *Perilomia*, *Salazaria*, and *Harlanlewisia*) (SC)
SPARTOTH = *Spartothamnella* Briq. (CH)
TECTONA = *Tectona* L. f. (TEC)
TEIJSMAN = *Teijsmanniodendron* Koord. (TEI)
TETRACLE = *Tetraclea* A. Gray (AJ, CL)
TEUCRIDI = *Teucridium* Hook. f. (CL)
TEUCRIUM = *Teucrium* L. (including *Kinostemon* Kudo) (AJ)
TINNEA = *Tinnea* Kotschy ex Hook. f. (AJ)
TRICARIZ = *Trichostema arizonicum* A. Gray (AJ)
TRICCHRO = *Trichostema* L. sect. *Chromocephalum* F. Lewis (AJ)
TRICORTH = *Trichostema* L. sect. *Orthopodium* Benth. (including *Isanthus* Michaux) (AJ)
TRICPURP = *Trichostema purpusii* Brandegee (AJ)
TRICTRIC = *Trichostema* L. sect. *Trichostema* (AJ)
TSOONGIA = *Tsoongia* Merr. (VI)
VITEX = *Vitex* L. (VI)
VITICIPR = *Viticipremna* H. J. Lam (VI)
WESTRING = *Westringia* Smith (PR)
WRIXONIA = *Wrixonia* F. Muell. (PR)

ified in Table 3) were treated as ordered because there was a reasonable basis to hypothesize a transformation series. For example (character 1), it is unlikely that an annual plant (state 2) would evolve directly from a tree or shrub (state 0), or vice versa, without passing through an herbaceous or subligneous perennial stage (state 1).

In an intergeneric study of this magnitude, it is

TABLE 3. Characters used in cladistic analysis. Character type (multistate characters only): ORD, ordered; UNO, unordered. *, hypothesized ancestral state (none designated when polarity assessment through outgroup comparison was not possible; see text).

1. (ORD) Habit: 0, woody plant; 1, herbaceous perennial or subshrub (i.e., woody only at very base); 2, annual or biennial.
2. If leaves not glabrous, multicellular trichomes present: 0, yes; 1, no (i.e., all trichomes unicellular). If leaves glabrous, character scored as missing.
3. Branched, multicellular trichomes present anywhere on plant: 0*, no; 1, yes. If plant entirely glabrous, character scored as missing.
4. Leaves bear subsessile glandular trichomes with a unicellular cap: 0, no; 1, yes.
5. Anisocytic stomata on leaves: 0, absent; 1, present.
6. (ORD) Diacytic types of stomata on leaves: 0, absent; 1, simple diacytic, but not diallelocytic, present; 2, both diacytic and diallelocytic present.
7. (UNO) Phyllotaxy: 0, opposite; 1, helical (alternate); 2, whorled.
8. (UNO) Leaf Structure: 0*, simple, unlobed; 1, three-lobed; 2, palmately lobed (more than 3 lobes); 3, pinnately lobed (more than 3 lobes); 4, once ternately compound; 5, once palmately compound (more than 3 leaflets); 6, once pinnately compound (more than 3 leaflets); 7, twice ternately compound. If there is developmental variation on a specimen, the higher state is assigned. Exception (not known to occur): if palmate and pinnate construction were to co-occur on the same specimen the character would be scored as variable.
9. Inflorescence a head: 0, no; 1, yes.
10. Inflorescence structure, if not a head: 0, axillary cymes or panicles or a thyrse (including "verticillate"); 1, flowers solitary in axils of foliage leaves or forming a raceme or spike. If inflorescence a head, character scored as missing.
11. Peduncles or pedicels within the cymules bear bractlets (excluding the bract or leaf subtending the cymule): 0, yes; 1, no.
12. Floral symmetry: 0, actinomorphic (i.e., corolla radially symmetrical and stamens isomerous and equal in length); 1*, zygomorphic (corolla or androecium not as above).
13. Calyx opening freely at anthesis: 0*, yes; 1, no, the elongating corolla forces its way through the fleshy or leathery, unlobed, hoodlike calyx, tearing it into lobes of irregular number and shape.
14. (UNO) Calyx symmetry: 0-2, radially symmetrical or nearly so: 0, four-lobed; 1, five-lobed; 2, with six or more lobes. 3-7, bilaterally symmetrical: 3, three-lobed upper lip and two-lobed lower lip; 4, two-lobed upper lip and two-lobed lower lip; 5, one-lobed upper lip and two-lobed lower lip; 6, one-lobed upper lip and four-lobed lower lip; 7, one-lobed upper lip and one-lobed lower lip. If calyx unlobed (truncate) or absent, character scored as missing.
15. Calyx with scutellum: 0*, no; 1, yes.

TABLE 3. Continued.

16. Flowering calyx gibbous: 0*, no; 1, yes.
17. Calyx with a ring of long trichomes in tube: 0*, no; 1, yes.
18. (ORD) Lobes of flowering calyx: 0, rounded to obtuse (including rounded and mucronate); 1, acute to attenuate; 2, spine-tipped or aristate; 3, uncinate. If calyx absent or unlobed, character scored as missing.
19. Fruiting calyx is closed apically by reflexing of one or both lips, enclosing fruit inside: 0*, no; 1, yes.
20. Fruiting calyx is closed apically by some other method, enclosing fruit inside: 0, no; 1, yes.
21. Fruiting calyx greatly inflated, bladderlike: 0*, no; 1, yes.
22. Fruiting calyx enlarged, patelliform: 0*, no; 1, yes.
23. Fruiting calyx enlarged, with elongate, winglike lobes: 0*, no; 1, yes.
24. Fruiting calyx enlarged, with elongate, plumose lobes: 0*, no; 1, yes.
25. Corolla in bud stalked, expanding abruptly on anterior (abaxial) side only; 0*, no; 1, yes.
26. (UNO) Corolla shape: States 0–3 are actinomorphic. 0, limb with four similar lobes; 1, limb with five similar lobes; 2, limb with six or more similar lobes; 3, corolla lacking lobes (tube truncate). States 4–8 are zygomorphic but not lipped (i.e., some lobes differ from others in size or shape, but all arise at the same level on the tube). 4, limb with four similar lobes, the other (anteriormost) different in shape and usually larger; 5, limb with three similar lobes, and the other (anteriormost) larger; 6, limb with three similar lobes, the other (posteriormost) larger; 7, limb with two posterior lobes of one sort and three anterior lobes of a different shape or size; 8, lobes of three shapes and/or sizes, the two posterior ones of one sort, the two lateral ones of another sort, and the anterior lobe of a third sort. States 9, A, B are bilabiate (i.e., the sinus separating the two lips is deeper than the sinuses separating the lobes on one or both lips). 9, posterior lip two-lobed, anterior lip three-lobed; A, posterior lip three- to four-lobed, anterior lip one-lobed; B, both lips one-lobed. States C–E are unilabiate. C, all lobes fall on posterior lip; D, all lobes fall on anterior lip and are similar in size and shape; E, all lobes fall on anterior lip, the middle lobe larger than the other four.
27. Corolla tube gibbous: 0, no; 1, yes.
28. Corolla tube curved: 0, no; 1, yes.
29. (UNO) Interior of corolla: 0, glabrous or nearly so; 1, with an incomplete annulus; 2, with a complete annulus; 3, densely pubescent on most or all of surface.
30. Anteriormost corolla lobe fimbriate: 0*, no; 1, yes.
31. (ORD) Shape of upper (posterior) lip of corolla: 0*, flat; 1, slightly galeate; 2, strongly galeate.
32. Corolla persistent, its expanded base forming a sheath covering the fruit: 0, no; 1, yes.
33. (ORD) Number of stamens: 0, two or four; 1, five; 2, more than five.
34. If less than five stamens, posterior pair reduced to

TABLE 3.   Continued.

staminodes or absent: 0*, no (i.e., posterior pair fertile or five or more stamens present); 1, yes.

35. If less than five stamens, anterior pair reduced to staminodes or absent: 0*, no (i.e., anterior pair fertile or five or more stamens present); 1, yes.

36. Stamen insertion: 0, in corolla tube; 1, at or very near the rim of the tube, where the lobes diverge.

37. (ORD) Relative length of stamens if at least four fertile stamens present: 0, anterior pair longest; 1, all stamens approximately the same length; 2, posterior pair longest. If only two fertile stamens present, character scored as missing.

38. Anterior stamens, if fertile, dimidiate (i.e., one theca of each stamen consistently aborted): 0*, no; 1, yes. If anterior pair sterile or absent, character scored as missing.

39. Posterior stamens, if fertile, dimidiate: 0*, no; 1, yes. If posterior pair sterile or absent, character scored as missing.

40. (ORD) Anther locule confluence at dehiscence: 0*, locules fully distinct or stamens dimidiate; 1, locules confluent but recognizable as two; 2, locules totally merged, appearing as one locule.

41. Thecae of the same anther (if not dimidiate or fully fused) similar in size and shape: 0, yes; 1, no. If stamens dimidiate or anther thecae fully fused, character scored as missing.

42. Anther theca orientation: 0, parallel; 1, divergent. If connective elongate, stamens dimidiate, or locules fully merged, character scored as missing.

43. Anthers appendaged at base: 0, no; 1, yes.

44. Anther dehiscence aperture shape: 0*, a longitudinal slit; 1, a subterminal pore.

45. Anther dehiscence aperture ciliate: 0*, no; 1, yes.

46. Anther dehiscence aperture bordered by one or more small teeth: 0*, no; 1, yes.

47. Anther connective appendaged: 0*, no; 1, yes.

48. Anther connective elongate, the thecae widely separated or (if one theca missing) the sterile branch of the connective prolonged down or out from the filament: 0*, no; 1, yes.

49. Connective or its appendage cristate (i.e., bearded with a cluster of broad-based trichomelike projections): 0*, no; 1, yes.

50. (UNO) Orientation of stamen filaments: 0, straight or only slightly curved or irregularly twisted; 1, strongly curved toward anterior of flower; 2, strongly curved toward posterior of flower; 3, strongly curved laterally. If there is variation among the stages of anthesis between state 0 and one of the other states, only the latter is assigned.

51. Stamen filaments bearded: 0, at base only or not at all; 1, in the middle and/or upper portions of the filament.

52. Filaments markedly dilated apically: 0*, no; 1, yes.

53. Filament extends beyond anther: 0*, no; 1, yes.

54. Ovary elevated on elongate gynophore above level of rest of disk: 0*, no; 1, yes.

55. Gynoecial structure: 0*, ovary unlobed or, if lobed,

TABLE 3.   Continued.

then the lobes not as in state 1; 1, ovary lobes wholly free from each other but laterally attached to a more or less elongate upward extension of the disk that terminates between them.

56. Elongation of ovary lobes during fruit development: 0*, the free (lobed) portion of the ovary does not elongate greatly relative to the fused portion (or ovary not lobed); 1, the free (lobed) portion of the ovary elongates greatly during fruit maturation.

57. (ORD) Depth of ovary lobing (if character 55 = 0): 0*, unlobed; 1, divided up to ¾ of the way to the base to form four lobes; 2, divided more than ¾ of the way to the base, the style thus gynobasic. If character 55 = 1, character 57 is scored as missing due to uncertainties about homology.

58. Nectary disk below ovary: 0, absent or poorly developed; 1, well developed.

59. (UNO) Number of vertically elongate lobes on nectary disk: 0*, none (or no disk); 1, one; 2, two; 3, three; 4, four.

60. Style persists after abscission of corolla: 0, no; 1*, yes.

61. (UNO) Style pubescence: 0*, glabrous; 1, pubescent only in the lower half of the unlobed portion; 2, pubescent only in the upper half of the unlobed portion; 3, pubescent in most or all of unlobed portion.

62. (ORD) Relative length of lobed versus unlobed portion of style-stigma complex: 0, unlobed portion more than 3 times the length of the lobes; 1, unlobed portion 1–3 times the length of the lobes; 2, unlobed portion shorter than the lobes.

63. (UNO) Relative length of lobes of style-stigma complex: 0, lobes equal or nearly so; 1, lobes distinctly unequal in length; 2, unlobed.

64. Shape of lobes of style-stigma complex: 0, linear or lingulate; 1, at least one lobe enlarged due to elaboration of stigmatoid tissue.

65. Number of ovules in ovary: 0, more than four; 1*, four or fewer.

66. (UNO) Ovary structure as seen in cross section: 0, carpel walls do not recurve into the interior of the carpel; 1, carpel walls recurve into interior of carpel, the ovules borne on their margins; 2, as in state 1, but the ovules borne short of the carpel margins.

67. Placentation: 0*, axile (including subbasal) or intermediate between axile and parietal; 1, free-central.

68. Shape of embryo sac: 0*, micropylar lobe shorter than or equal to and/or narrower than the chalazal lobe; 1, micropylar lobe much longer and broader than the chalazal lobe.

69. (UNO) Fruit type: 0, dehiscent capsule; 1, indehiscent capsule, developing from 4-ovulate ovary, containing four seeds (or fewer due to ovule abortion); 2, indehiscent capsule, developing from 2-ovulate ovary, containing two seeds (or only one due to ovule abortion); 3, a single achene developing from a 1-ovulate ovary; 4, drupe with more than four 1-seeded pyrenes; 5, drupe, developing from 4-ovulate

TABLE 3. Continued.

ovary, with one pyrene containing four seeds (or fewer seeds by ovule abortion); 6, drupe, developing from 4-ovulate ovary, with two pyrenes, each normally containing two seeds; 7, drupe, developing from 4-ovulate ovary, with four 1-seeded pyrenes (or fewer pyrenes by ovule abortion); 8, drupe, developing from 2-ovulate ovary, with two 1-seeded pyrenes (or one pyrene by ovule abortion); 9, drupe, developing from 2-ovulate ovary, with one 2-seeded pyrene (or only one seed by ovule abortion); A, fruit separates into four fleshy 1-seeded mericarps (or fewer by ovule abortion); B, fruit separates into four dry 1-seeded mericarps ("nutlets") (or fewer by ovule abortion); C, fruit (from 4-ovulate ovary) separates into two dry 2-seeded nutlets (or fewer seeds by abortion); D, fruit (from 4-ovulate ovary) separates into two fleshy 2-seeded mericarps (or fewer seeds by ovule abortion). The few genera that have fruits that split into mericarps only with pressure were scored as intermediate between 1 and B or between 7 and A.

70. Surface of pericarp (if dry) or pyrene (if drupaceous) ridged, the ridges often forming a reticulum: 0, no; 1, yes.

71. (UNO) Surface of pericarp (if dry) or pyrene (if drupaceous) with tuberculate or elongate outgrowths: 0*, no; 1, outgrowths tuberculate, papilliform or verrucate; 2, outgrowths greatly elongate, usually plumose, developing during fruit maturation from papilliform outgrowths on ovary (probably homologous to outgrowths in state 1).

72. Pericarp (if dry fruit) highly lustrous, appearing polished: 0, no; 1, yes. If fruit fleshy, character scored as missing.

73. (UNO) Mericarp shape: 0, obovoid to obloid; 1, quarter-sphere; 2, boat-shaped; 3, nearly flat; 4, subspherical to spherical; 5, clavate; 6, trigonal; 7, boomerang-shaped (abruptly bent); 8, fusiform; 9, ovoid; A, lenticular; B, elongate and straight-sided; C, half-sphere.

74. Mericarps with lateral wings: 0*, no (or fruit not a schizocarp); 1, yes.

75. Mericarps with basal wing: 0*, no (or fruit not a schizocarp); 1, yes.

76. Mericarp attachment scar with reflexed spinelike projections: 0*, no; 1, yes.

77. Mericarp attachment scar with vertical membranaceous outgrowth: 0*, no; 1, yes.

78. Seed albuminous: 0, no; 1, yes.

79. (UNO) Embryo shape: 0, spatulate, straight or slightly curved; 1, abruptly bent but not doubled over; 2, doubled over on itself; 3, investing.

80. (UNO) Pollen sculpturing types: 0, psilate, microreticulate to tectate-perforate (tectum relatively even (vs. 1)); 1, tectate-perforate to microreticulate with muri exhibiting an alternation of distinctly raised and nonraised segments; 2, striato-reticulate; 3, rugulose; 4, suprareticulate to suprarugulose; 5, supraverrucate; 6, supraspinulose to spinose; 7, minutely su-

TABLE 3. Continued.

praspinulose or supragranulate (the projections no more than 0.1 μm long); 8, suprareticulate-spinose; 9, bearing irregular, blunt supratectal protuberances.

81. (UNO) Pollen aperture type: 0, colpate; 1, colporate; 2, porate.

82. Pollen colpi operculate: 0*, no; 1, yes.

83. (UNO) Number of pollen apertures: 0*, three; 1, four; 2, five; 3, six to eight, zonocolpate; 4, six-pantocolpate.

84. (UNO) Structure of columellate stratum of exine: 0*, with simple columellae; 1, with branched to granular columellae; 2, massive, undifferentiated.

85. Allenic component (probably laballenic acid) present in the seed oils: 0*, no; 1, yes.

not feasible to examine every species. For small genera, the morphology of most or all species has been studied, but larger genera have been sampled using an exemplar method. Before initiating data collection for a large genus, available monographs and revisions were consulted, as well as basic works such as Briquet's treatments of the Verbenaceae (1895) and Labiatae (1895–1897). Based on accepted infrageneric classifications, a sample was selected to encompass most or all of the morphological variation in the genus. For example, in the case of *Teucrium*, with ca. 200 species, the 37 species chosen for examination included representatives of every previously recognized infrageneric grouping and every major portion of its geographic range.

When variation was encountered within an OTU, the character was scored as uncertain except in those few cases in which it was possible to assess with confidence the ancestral state within the taxon. For example, it is clear that the ostensibly primitive drupaceous fruit in *Ajuga postii* Briq. is secondarily derived, because the distribution of other characters shows that this species is far from basal within the genus. As a result, only state B (dry nutlets) was scored for character 69 in *Ajuga*.

Scorings of "uncertain" and "missing" are treated differently in the parsimony package used in this analysis (PAUP version 3.0L; Swofford, 1990). If a character state is scored as missing ("?" in the data matrix) for a taxon, it will be assigned whichever state is most parsimonious given the placement of the taxon on the tree by the other characters. If a character is scored as uncertain (i.e., two or more states are assigned to the taxon in the data matrix), the algorithm will choose from among the assigned states the one that min-

imizes the overall tree length. Thus, an uncertain state plays a role in determining the tree topology, while a missing state does not. This is an important distinction for multistate characters. For example, if only two of the ten possible states of character 80 occur within a taxon, scoring it as uncertain rather than missing prevents the algorithm from assigning a state that is known *not* to occur in the OTU.

There are two situations other than intra-OTU variation that resulted in scoring a character as "uncertain": character state intermediacy and true uncertainty. An example of the first situation can be found in *Caryopteris grata*, in which the slightly fleshy fruit contains four pyrenes. The fruit usually does not split spontaneously (at least in herbarium material) but can be broken apart with slight thumb pressure to form four mericarps. Because the fruit is intermediate between a drupe and a fleshy schizo-carp, character 69 was scored as intermediate ("uncertain") between states 7 and A.

An example of the second situation can be found in *Hosea*, in which the corolla has three similar lobes and one larger one, but it has not been possible to determine from the available herbarium material and published descriptions whether it is the anterior or posterior lobe that is enlarged. If character 26 (corolla shape) were binary, the state would simply have been scored as missing for *Hosea*. However, since the true corolla shape could be narrowed down to two of the 15 possible states, it was preferable to score the character as "uncertain," with states 5 and 6 listed as the only possibilities.

A character was scored as missing for a taxon under two circumstances: (1) the information was indeed missing (i.e., *any* of the possible states could occur in the taxon); (2) the character is inapplicable to the taxon. For example, if the calyx is unlobed, character 18 (calyx lobe shape) is inapplicable and was scored as missing.

Because of its length, the data matrix has been excluded from this report. It is on file in the libraries of the Harvard University Herbaria and the Royal Botanic Gardens at Kew, and copies are available from the author on request.

OUTGROUPS

The closest outgroups are those Verbenaceae *sensu lato* that lie outside the study group—viz., subfamily Verbenoideae and the segregate families Cyclocheilaceae, Nesogenaceae, Phrymaceae, and Stilbaceae. The Scrophulariales, the closest relatives of the Verbenaceae *sensu lato* and Labiatae (discussed below), constitute a second, more distant

set of outgroups. The forenamed segregate families are treated here as close outgroups under the assumption that the Verbenaceae *sensu lato* plus the Labiatae form a clade. Upon further study, however, it may turn out that some of these segregate families originated from different scrophularialean lineages than the rest of the Verbenaceae. Their inclusion among the primary outgroups, if incorrect, may have prevented polarity assessment for some characters due to variation among the outgroups, but it should not have resulted in incorrect polarities, as agreement among all five primary outgroups was required for polarity assessment.

Because data collection for both sets of outgroups is still incomplete, they were not included in the data set. Rather, the results of this analysis have been left as an undirected tree, but the most plausible rooting positions have been determined a posteriori based on those characters for which data are available for the outgroups (i.e., Lundberg Rooting; Lundberg, 1972). The hypothesized ancestral states used in the rooting procedure are indicated with an asterisk in Table 3.

A close relationship to the Verbenaceae and Labiatae has been claimed for the Boraginaceae (Cronquist, 1981) and the Scrophulariales (Dahlgren, 1977; Wagenitz, 1977; Cantino, 1982b). The former hypothesis is based primarily on a suite of related gynoecial features, while the latter is supported by a variety of chemical, embryological, and morphological characters. Recent molecular studies corroborate the Scrophulariales hypothesis. Both sequence data for the *rbc*L gene (Olmstead et al., 1992, in press) and restriction site data for the inverted repeat of the chloroplast genome (Downie & Palmer, 1992) delimit a major clade comprising the Scrophulariales *sensu* Cronquist (1981) plus the Verbenaceae, Labiatae, and Callitrichaceae. The two molecular studies disagree, however, on the precise position of the Verbenaceae and Labiatae within this clade. Acanthaceae, Bignoniaceae, Buddlejaceae, Callitrichaceae, Gesneriaceae, Myoporaceae, Pedaliaceae, and Scrophulariaceae are placed relatively close to the Verbenaceae and Labiatae by one or both studies, with Oleaceae more distantly related.

A recent cladistic analysis based mainly on morphological data (Lu, 1990) concluded that the sister group of the Verbenaceae–Labiatae clade is a group composed of Phrymaceae (included in Verbenaceae by Cronquist, 1981), Trapellaceae (included in Pedaliaceae by Cronquist, 1981), Hippuridaceae, Callitrichaceae, and Hydrostachyaceae, with Mendonciaceae and Thunbergiaceae (both frequently included in the Acanthaceae) the next closest groups.

Unfortunately, flaws in character scoring and polarity assessment in this paper render these conclusions questionable. For example, the single synapomorphy cited by Lu (1990) as linking the Verbenaceae–Labiatae clade to its sister group is loss of diacytic stomata. However, diacytic stomata are widespread in the Verbenaceae and occur in nearly all genera of Labiatae (Cantino, 1990a).

Other problems in Lu's analysis include the scoring of Labiatae as having an actinomorphic corolla and Verbenaceae as having alternate leaves. What may appear to be simple errors in the data matrix actually result from Lu's handling of variation within the unit taxa. If more than one state occurs in a family, only the plesiomorphic state was assigned. Although this procedure is correct, it requires that proximal outgroups be used. In Lu's analysis, polarity assessments were based on the outgroups to the Lamiiflorae as a whole (viz., Oleaceae, Clethraceae, and Solanaceae) rather than on the immediate relatives of the OTU in which the variation occurred. Thus an actinomorphic corolla, which is clearly a reversal from a primitively zygomorphic condition within the Labiatae, was treated as plesiomorphic and assigned to the family as a whole. Similarly, spiral phyllotaxy ("alternate leaves") is a rare and probably derived condition within the Verbenaceae. A better approach when dealing with variation within OTUs is to attempt to determine the basal state within the taxon or, if this is not possible, score the taxon as uncertain for that character and allow the parsimony algorithm to assign the character state that minimizes the overall tree length.

Based on the above considerations, the best candidates for sister group of the Verbenaceae–Labiatae clade are Acanthaceae sensu lato, Bignoniaceae, Buddlejaceae, Callitrichaceae, Gesneriaceae, Myoporaceae, Pedaliaceae, and Scrophulariaceae. All of these except the Callitrichaceae were used as secondary outgroups when assessing the most likely positions for the root of the undirected tree, but greater emphasis was placed on the primary outgroups (i.e., Verbenoideae and the segregate families of Verbenaceae sensu lato).

CLADISTIC ANALYSIS

The analysis was carried out using PAUP version 3.0L (Swofford, 1990) on a MacIntosh IIfx computer. All three branch-swapping algorithms used by PAUP were employed in an attempt to find the most parsimonious trees. In order to test the relative parsimony of the hypothesis that the Labiatae are monophyletic, a second analysis was carried out with the data set constrained such that only trees in which the Labiatae form a clade were saved.

When optimizing characters on the trees, the delayed transformation option, which favors parallelisms over reversals when they are equally parsimonious, was used in most cases. The accelerated transformation option was used in a few instances (see Results and Discussion) when the character state distribution within an OTU suggested that the internal variation was more likely due to reversal than parallelism. The tree topology and overall parsimony are not affected by the choice of optimization routine, but the positions of certain character transformations are altered.

RESULTS AND DISCUSSION

The shortest trees found by PAUP are 399 steps long, with a consistency index (CI) of 0.298 (autapomorphies were excluded from these calculations, although they have been mapped onto the consensus tree). The low CI value is due in part to the large number of OTUs in the analysis. Sanderson & Donoghue (1989) found consistency index to be highly correlated with number of taxa. The largest data sets in their study included 65–68 taxa and had CI values of 0.32–0.37. Thus, a CI of 0.298 in an analysis that includes 106 taxa is not unreasonably low. Indeed, when the data matrix in the present study was cut in half by deleting alternate entries in the alphabetical list of taxa and the analysis was rerun with the remaining 53 taxa, the CI was 0.46. When the matrix was reduced to 27 taxa by the same procedure, the CI rose to 0.55. These figures are all close to the regression line in Sanderson and Donoghue's study.

Although the exact number cannot be determined, it is clear that there are a great many equally parsimonious trees. PAUP found 4,100 399-step trees before the analysis was aborted due to overflow of the tree buffer, and it is possible that many more exist. In spite of the existence of many equally parsimonious trees, there is a high degree of resolution in some parts of the strict consensus tree based on them (Fig. 1).

Space limitations preclude mapping of the character state changes onto the full consensus tree. Rather, they have been separately mapped (Figs. 2–4) onto the three large groups labeled A, B, and C in Figure 1. Because no outgroups were included in the data set, the consensus tree was initially undirected and is shown as such in Figure 1. How-
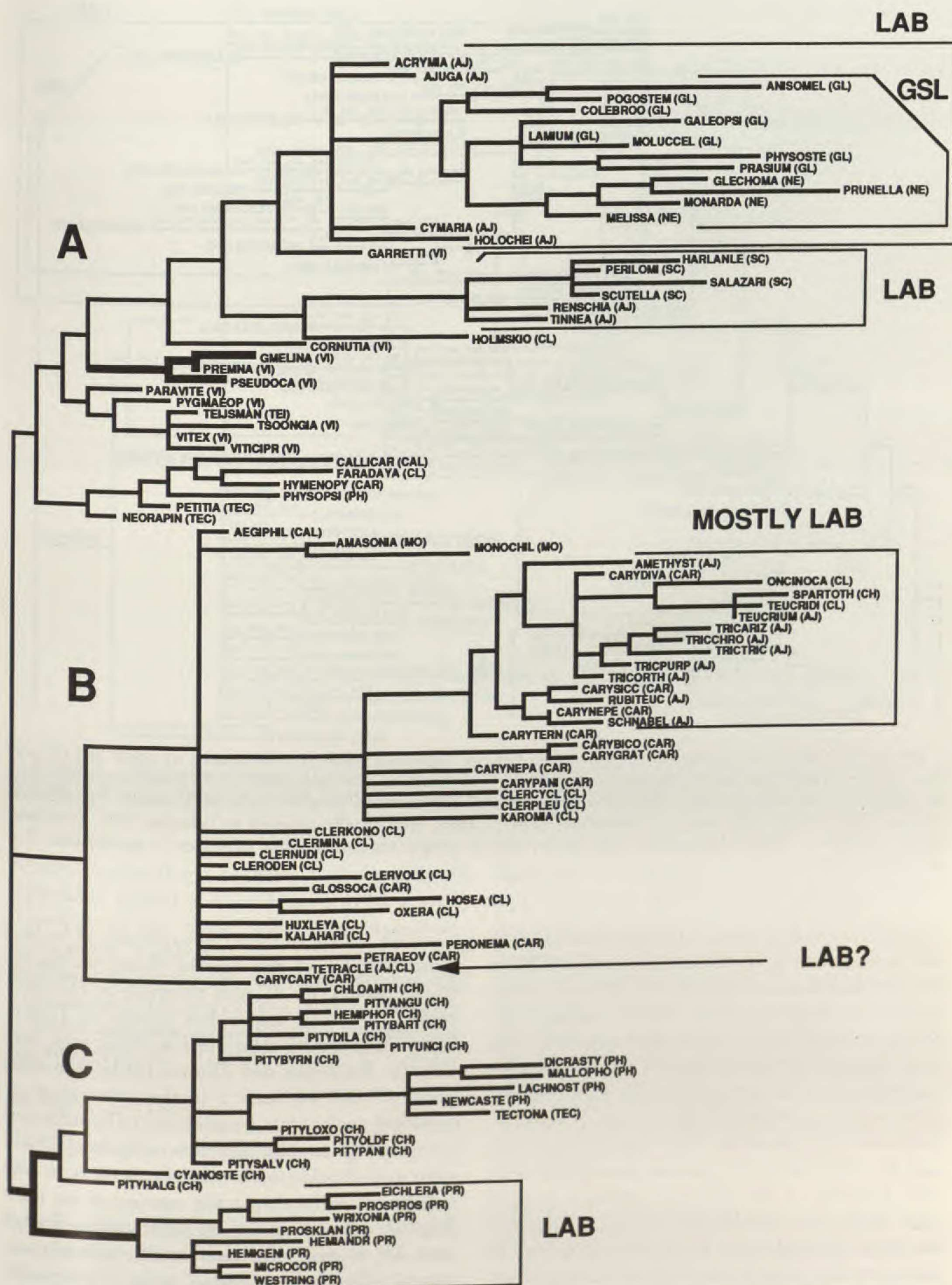
FIGURE 1. Strict consensus tree (undirected) based on 4,100 399-step trees. Thickened stems indicate positions where the tree most likely roots (see text). Branch lengths are proportional to the number of character changes. See Table 2 for full names of OTUs. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. A, B, C: groups discussed in text. LAB, taxa usually assigned to Labiatae; GSL, gynobasic-styled Labiatae.
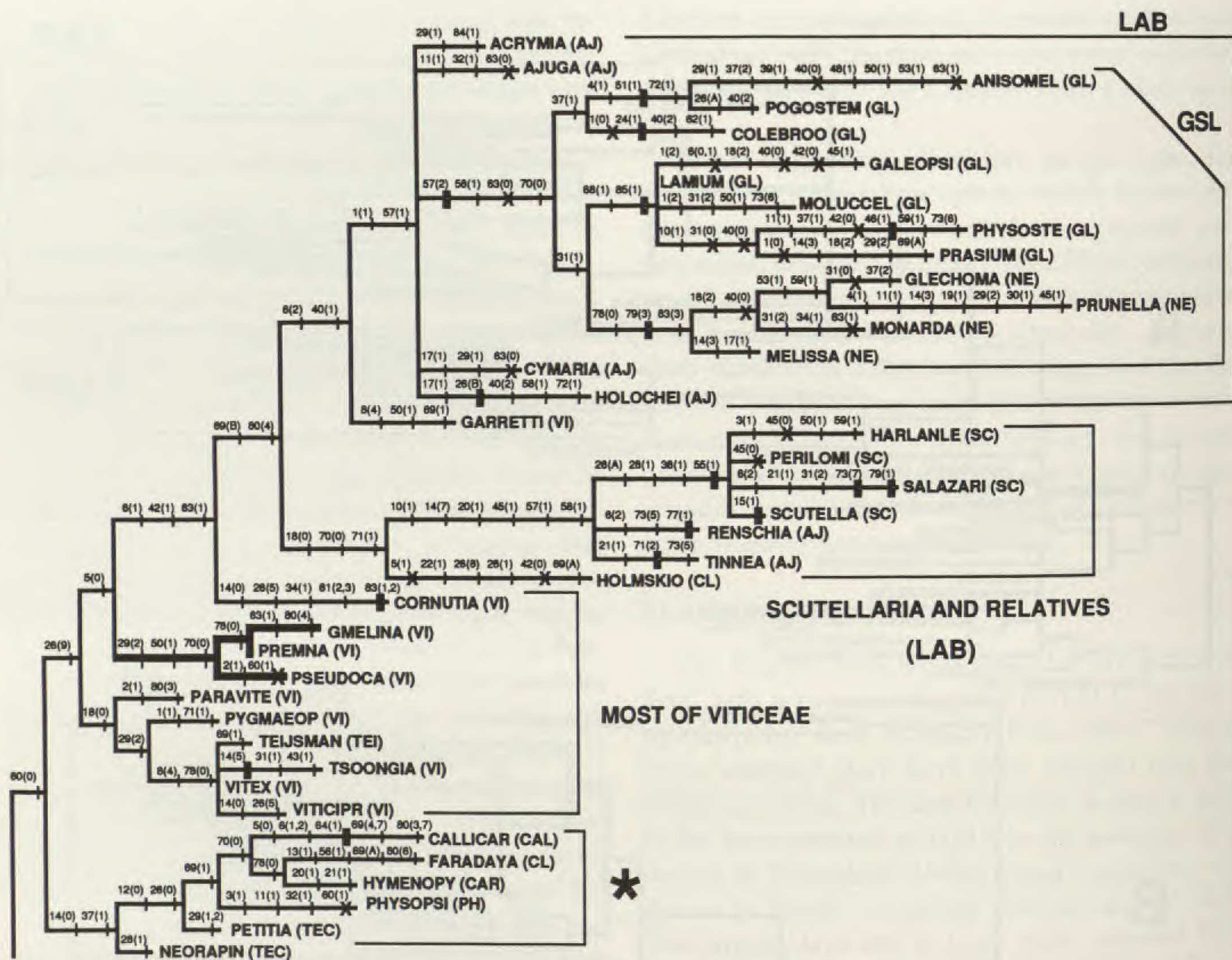
FIGURE 2. Character changes in Group A (see Fig. 1). Character states are designated by digits and (if more than 10 states) letters. Because the tree as a whole may root in the region designated by thickened stems (see text), the polarity of character changes within this zone and on the three stems basal to it may be incorrect. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. LAB, taxa usually assigned to Labiatae; GSL, gynobasic-styled Labiatae; *, group discussed in text. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

ever, some rooting positions are more plausible than others, based on the limited data presently available for the outgroups. Using the Lundberg Rooting approach (Lundberg, 1972), with the outlying Verbenaceae sensu lato as the primary outgroups and some families of Scrophulariales as more distant outgroups (see Outgroups above), eight equally parsimonious positions for the root have been hypothesized (designated by thick lines in Figs. 1, 2, and 4), which lie in two separate parts of the tree. The polarities of the character changes mapped onto these two hypothesized rooting regions and the three internodes that lie between them may be incorrect, but changes elsewhere on the strict consensus tree represent hypothesized synapomorphies.

For the most part, the delayed transformation option was used when mapping characters onto Figures 2–4, but accelerated transformation was used in the following instances: (1) State 1 of char-

acter 45 (ciliate anthers) is hypothesized to be a synapomorphy of the *Tinnea–Renschia*–Scutellarieae clade (Fig. 2), with reversals in *Harlanlewisia, Perilomia,* and a few species of *Tinnea,* rather than arising separately in *Salazaria, Scutellaria, Renschia,* and *Tinnea.* (2) In both characters 47 and 49, state 1 (anther connective appendaged and cristate, respectively) is hypothesized to be a synapomorphy of a clade comprising *Eichlerago* and *Prostanthera* sect. *Prostanthera,* with subsequent reversal in a few species of the latter (Fig. 4), rather than arising separately in the two taxa. (3) State 7 of character 80 (minutely spinulose pollen) is hypothesized to be a synapomorphy of a clade comprising *Eichlerago, Wrixonia,* and both sections of *Prostanthera,* with subsequent reversal in some species of *Prostanthera* sect. *Klanderia* (Fig. 4). The delayed transformation option would place the origin of state 7 on the stem leading to *Wrixonia, Eichlerago,* and *Prostanthe-*
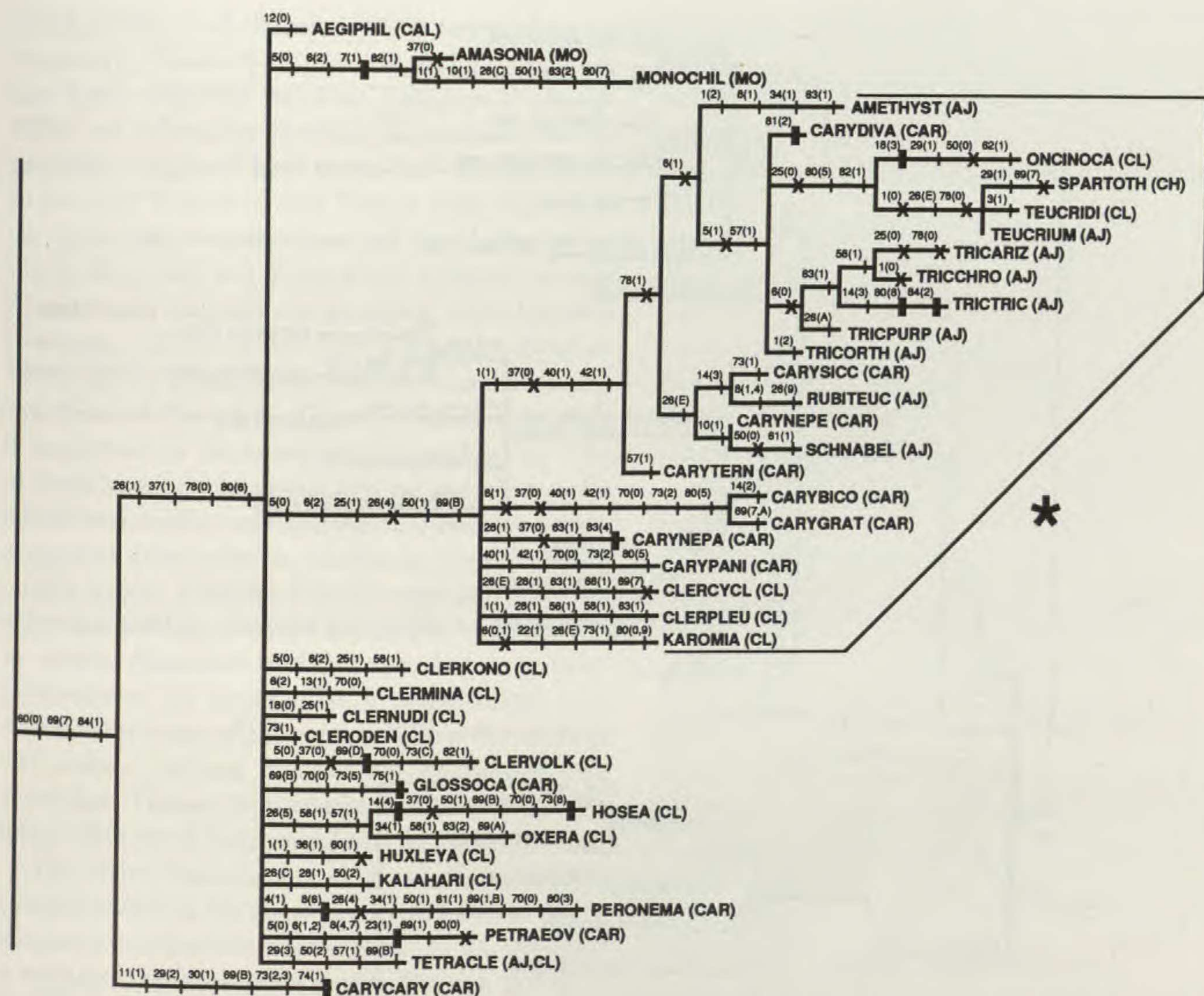
FIGURE 3. Character changes in Group B (see Fig. 1). Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. *, group discussed in text. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

ra sect. *Prostanthera*. (4) State 1 of character 82 (operculate pollen) is hypothesized to be a synapomorphy of the clade comprising *Dicrastylis*, *Mallophora*, *Lachnostachys*, *Newcastelia*, and *Tectona*, with subsequent reversal in *Tectona* and a few species of *Dicrastylis* and *Newcastelia*, rather than arising independently in the first four genera listed (Fig. 4).
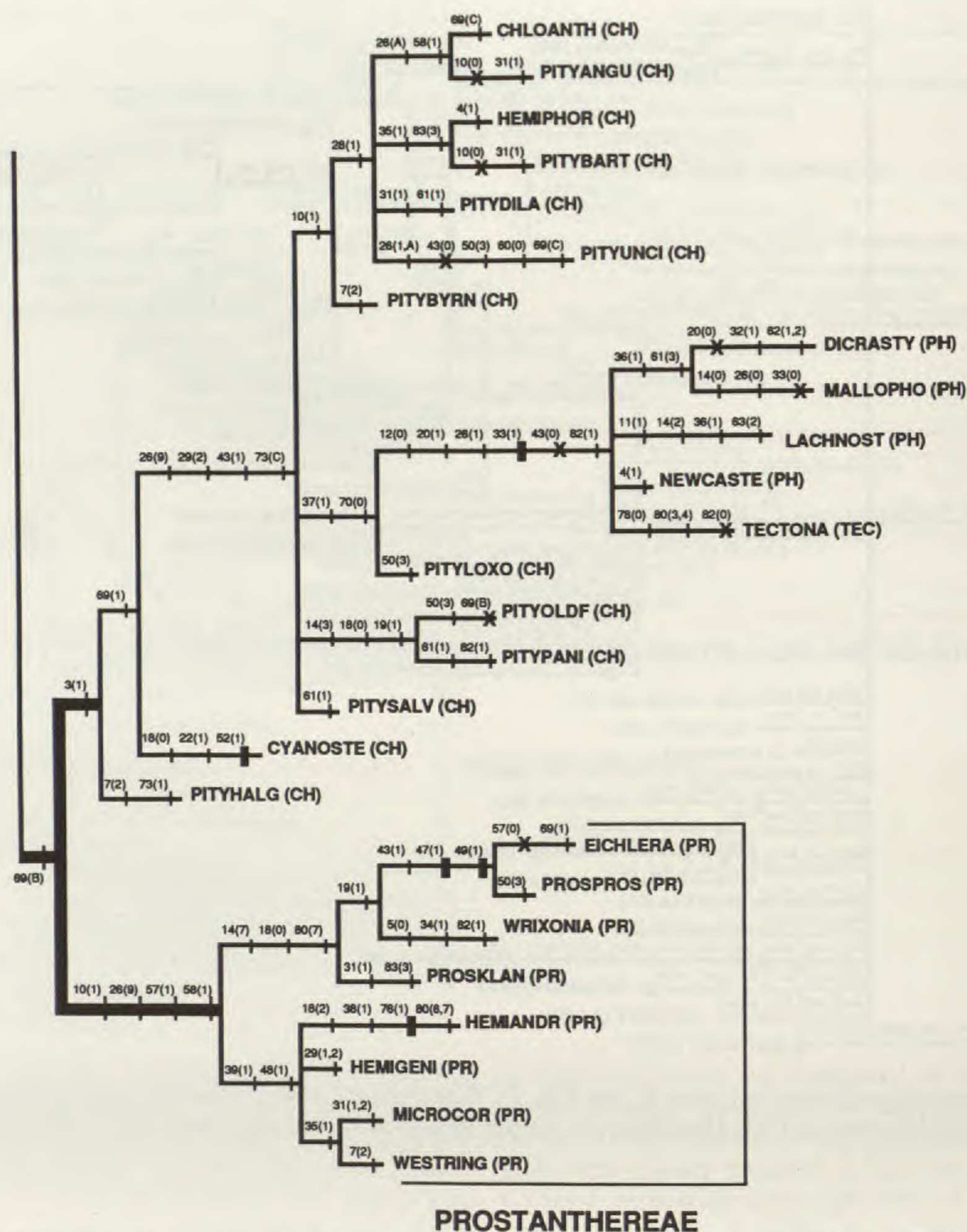
POLYPHYLY OF LABIATAE

The hypothesis that the Labiatae are polyphyletic is strongly supported by this analysis. The strict consensus tree (Fig. 1) requires at least four separate origins of the Labiatae from the Verbenaceae, in three widely separate parts of the tree. When the Labiatae were constrained to form a monophyletic group, the shortest trees required 412 character changes—13 steps longer than the most parsimonious trees without this constraint.

The four groups of Labiatae that emerge as distinct in the strict consensus tree ("LAB" in Fig. 1) are composed of: (1) the gynobasic-styled La-

biatae plus four genera of Ajugeae (*Ajuga*, *Acrymia*, *Cymaria*, and *Holocheila*); (2) tribe Scutellarieae plus *Renschia*, and *Tinnea*; (3) *Amethystea*, *Rubiteucris*, *Schnabelia*, *Teucrium*, and *Trichostema* (because three species of *Caryopteris* and three other genera of Verbenaceae are included in this clade as well, more than one origin of the labiate genera within the group is likely); and (4) tribe Prostanthereae. In addition, *Tetraclea* (placed in the Labiatae by some authors and the Verbenaceae by others) is unconnected to the other groups of Labiatae.

GYNOBASIC-STYLED LABIATAE
AND THEIR RELATIVES

With the exception of a few species in tribe Scutellarieae (discussed below), the gynobasic-styled Labiatae ("GSL" in Figs. 1 and 2) form a monophyletic group. Although this major clade is represented by only 12 genera here, it comprises about 90% of the Labiatae. It is nested within a larger clade characterized by suprareticulate pollen and

CHLOANTH (CH)
69(C)
26(A) 58(1)
10(0) 31(1)
PITYANGU (CH)
4(1) HEMIPHOR (CH)
35(1) 83(3)
28(1)
10(0) 31(1)
PITYBART (CH)
31(1) 61(1) PITYDILA (CH)
10(1)
26(1,A) 43(0) 50(3) 60(0) 69(C) PITYUNCI (CH)
7(2) PITYBYRN (CH)

20(0) 32(1) 62(1,2)
DICRASTY (PH)
36(1) 61(3)
14(0) 26(0) 33(0) MALLOPHO (PH)
12(0) 20(1) 26(1) 33(1) 43(0) 82(1)
11(1) 14(2) 36(1) 83(2) LACHNOST (PH)
26(9) 29(2) 43(1) 73(C)
4(1) NEWCASTE (PH)
37(1) 70(0)
78(0) 80(3,4) 82(0) TECTONA (TEC)
50(3) PITYLOXO (CH)
69(1)
50(3) 69(B) PITYOLDF (CH)
14(3) 18(0) 19(1)
61(1) 82(1) PITYPANI (CH)
3(1)
61(1) PITYSALV (CH)
18(0) 22(1) 52(1) CYANOSTE (CH)
7(2) 73(1) PITYHALG (CH)

69(B)
57(0) 69(1)
EICHLERA (PR)
43(1) 47(1) 49(1)
50(3) PROSPROS (PR)
19(1)
5(0) 34(1) 82(1) WRIXONIA (PR)
14(7) 18(0) 80(7)
31(1) 83(3) PROSKLAN (PR)
10(1) 26(9) 57(1) 58(1)
18(2) 38(1) 76(1) 80(6,7) HEMIANDR (PR)
29(1,2) HEMIGENI (PR)
39(1) 48(1)
31(1,2) MICROCOR (PR)
35(1)
7(2) WESTRING (PR)

PROSTANTHEREAE

FIGURE 4. Character changes in Group C (see Fig. 1). Because the tree as a whole may root in the region designated by thickened stems (see text), the polarity of character changes within this zone may be incorrect. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

a fruit composed of nutlets, which includes (in addition to the gynobasic-styled Labiatae) tribe Scutellarieae, six genera of Ajugeae, and the verbenaceous genera *Garrettia* and *Holmskioldia*. This larger clade arises out of a verbenaceous assemblage comprising most of tribe Viticeae plus *Teijsmanniodendron* (Caryopteridoideae).

Although the Scutellarieae are traditionally grouped with the gynobasic-styled Labiatae, the style is truly gynobasic only in some species of *Perilomia* and a few (perhaps only one) species of *Scutellaria* sensu stricto (viz., *S. nummulariifolia* Hook. f.). In the rest of *Scutellaria* and *Perilomia*, as well as in *Salazaria* and *Harlanlewisia*, the ovary lobes are wholly free from each other but are laterally attached to a more or less elongate upward extension of the disk. The style is attached

to the ovary lobes above the apex of the disk extension and is thus not truly gynobasic. Because this gynoecial morphology could have evolved from either a shallowly lobed ovary (character 57 = 1; e.g., tribe Ajugeae) or the sort of gynoecium found in the gynobasic-styled Labiatae (character 57 = 2), character 57 was coded as missing for the Scutellarieae. As it turned out, the most parsimonious hypothesis groups the Scutellarieae with two genera (viz., *Renschia* and *Tinnea*) that have a shallowly lobed ovary (Fig. 2), implying that the gynobasic style that occurs in a few species of *Perilomia* and *Scutellaria* arose independently from that in the other gynobasic-styled Labiatae.

A close relationship among the four genera of Scutellarieae (viz., *Scutellaria*, *Salazaria*, *Perilomia*, and *Harlanlewisia*) is well accepted (Epling,

1942, 1955), and Paton (1990) treats them as congeneric. Similarly, *Renschia* and *Tinnea* have long been regarded as close relatives (Vollesen, 1975 and references therein). In contrast, the relationship suggested here between *Scutellaria* sensu lato and *Renschia* and *Tinnea* runs counter to the prevailing classifications of the Labiatae, in which *Renschia* and *Tinnea* are assigned to tribe Ajugeae and *Scutellaria* to either tribe Lamieae (Bentham, 1876) or its own subfamily (Briquet, 1895–1897; Wunderlich, 1967). Nonetheless, the hypothesized *Renschia–Tinnea*-Scutellarieae clade is supported by six synapomorphies (Fig. 2). Two of these concern its distinctive calyx, which is bilabiate with entire, rounded lips that become tightly appressed after anthesis, enclosing the developing nutlets inside. Vollesen (1975) suggested that this calyx morphology evolved separately in *Scutellaria* versus *Renschia* and *Tinnea*, but it is more parsimonious to hypothesize a single origin in a common ancestor of these taxa. When the analysis was redone without these calyx characters, the *Renschia–Tinnea*-Scutellarieae clade remained intact, thus there is no circularity in this argument.

The strict consensus tree shows *Holmskioldia* (Verbenaceae) as the sister group of the *Renschia–Tinnea*-Scutellarieae clade (Figs. 1, 2), implying a separate verbenaceous origin for this group of Labiatae. *Holmskioldia* is monotypic as delimited here, comprising only the Asian species, *H. sanguinea* Retz. The African species formerly assigned to *Holmskioldia* are included here within *Karomia*, as by Fernandes (1985). The two genera do not appear to be closely related, *Karomia* falling in the central part of group B (Figs. 1, 3) and *Holmskioldia* in group A. Although a close relationship between *Scutellaria* and *Holmskioldia* has not previously been suggested, the fruit of *Holmskioldia* bears a distinctive tuberculate sculpturing very similar to that found in *Renschia* and most species of Scutellarieae. In *Tinnea*, the fruit bears long, usually plumose, trichomelike projections that elongate greatly during fruit maturation from tiny papillae on the ovary. Further investigations of the pericarp ornamentation in these genera using scanning electron microscopy (in progress) will help determine whether the structures are truly homologous.

OTHER "LABIATAE"

Another intriguing group that cuts across traditional taxonomic boundaries (marked with an asterisk in Fig. 3) comprises five genera of Ajugeae (Labiatae), parts of the genera *Caryopteris* (Ver-

benaceae, Caryopterideae) and *Clerodendrum* (Verbenaceae, Clerodendreae), three other genera of Clerodendreae, and *Spartothamnella* (Verbenaceae, Chloanthoideae). While it is tempting to dismiss such a taxonomically diverse assemblage as an artifact, the strong character support for this clade is noteworthy (Fig. 3). The most distinctive of its six synapomorphies is the shape of the flower bud, in which the corolla expands abruptly on the lower (anterior) side only, so that it looks something like a golf club. This feature is absent (presumably due to reversal) in *Trichostema arizonicum* and most members of the "teucrioid" subgroup.

The closest relatives of *Teucrium*, one of the largest and most widespread genera of Labiatae, are the verbenaceous genera *Teucridium*, *Spartothamnella*, and *Oncinocalyx*. My earlier suggestion (Cantino, 1990b) that *Monochilus* also belongs to this group is apparently incorrect, its affinities lying rather with *Amasonia* (near top of Fig. 3). This teucrioid clade, which is characterized by its distinctive operculate, verrucate pollen, deserves special comment because of the widely divergent taxonomic positions of its four genera. *Teucridium* and *Oncinocalyx* are members of tribe Clerodendreae (subfamily Viticoideae) (Briquet, 1895; Moldenke, 1971), while *Spartothamnella* is generally assigned to the Chloanthoideae (Briquet, 1895). Since the Chloanthoideae have been elevated to familial rank by some authors (Moldenke, 1971; Munir, 1976, 1979), the teucrioid clade draws its membership from what are currently treated as three different families.

Tribe Prostanthereae (Labiatae) is monophyletic in the strict consensus tree (Figs. 1, 4) and comprises two subgroups: (1) the prostantheroid clade, delimited by calyx morphology and pollen sculpturing, and (2) the hemigenioid clade with its peculiar androecial morphology (dimidiate stamens with an elongate connective). Within the former subgroup, *Prostanthera* is paraphyletic if *Eichlerago* and *Wrixonia* are segregated from it. The derived position of *Eichlerago* indicates that the ostensibly primitive unlobed ovary in *Eichlerago* represents a character reversal rather than a plesiomorphic condition.

Within the hemigenioid subgroup, *Hemigenia* is delimited by a single autapomorphy—an annulate corolla. However, a partial to complete annulus also occurs in some species of *Microcorys* and *Westringia*. In view of the weak character support for the monophyly of *Hemigenia*, a plausible alternative hypothesis is that it is a paraphyletic group that has given rise to both *Hemiandra* and the *Microcorys–Westringia* clade.

BROADER VIEW OF THE CONSENSUS TREE

The unrooted consensus tree can be divided into three large groups (A, B, and C in Fig. 1), at least two of which appear to be clades. The monophyly of Group B is supported by character 84, branched columellae (discussed below). It is unclear which of the other two groups represents a clade, because the consensus tree may be equally parsimoniously rooted near the base of groups A and C (Fig. 1). The three groups comprise: (A) the gynobasic-styled Labiatae, the Ajugeae (Labiatae) that have suprareticulate pollen, tribe Scutellarieae (Labiatae), tribe Viticeae (Verbenaceae), and eight other genera of Verbenaceae representing three subfamilies and six tribes (viz., Callicarpeae (1), Clerodendreae (2), Tectoneae (2), Caryopterideae (1), Teijsmanniodendreae (1), and Physopsideae (1)); (B) the Ajugeae that have spinulose or verrucate supratectal sculpturing, tribe Monochileae (Verbenaceae), *Aegiphila* (Callicarpeae), *Spartothamnella* (Chloantheae), and most genera of tribes Clerodendreae and Caryopterideae; (C) tribe Prostanthereae (Labiatae), most of subfamily Chloanthoideae (Verbenaceae), and *Tectona* (Verbenaceae, Tectoneae).

Group A is the most incongruent with the current classification of the two families and may be paraphyletic. An argument will be presented below that suggests that the true affinities of *Faradaya* and *Physopsis* are with Groups B and C, respectively, in spite of their assignment to Group A in the consensus tree.

Group B, although taxonomically diverse, is probably monophyletic. All but one of the genera of Labiatae and Verbenaceae that have spinulose or verrucate supratectal sculpturing fall within this group in the most parsimonious trees. (The affinities of the one exception, *Faradaya*, probably lie with this group as well; discussed below.) Only a few members of Group B have other sorts of exine ornamentation. Moreover, all but one of the taxa in Group B for which data are available have pollen with branched columellae (occasionally varying to granular), a feature that is very rare elsewhere in the Lamiales. The one exception, *Trichostema* sect. *Trichostema*, has a massive, undifferentiated columellate stratum, an autapomorphy. Branched columellae are not known to occur in the outgroups, thus their presence is hypothesized to be a synapomorphy of Group B.

With the exception of *Tectona*, Group C is an entirely Australian assemblage. A close relationship between *Tectona* and tribe Physopsideae (Chloanthoideae) may at first seem unlikely, inasmuch as

Tectona species are large Indomalaysian trees, while the Physopsideae are Australian shrubs. However, there are many derived similarities between these taxa (Fig. 4), including actinomorphic flowers with isomerous stamens, an indument of branched trichomes, and a fruiting calyx that is constricted apically, enclosing the fruit. Moreover, Carlquist (1981) noted that *Tectona* is one of only two non-chloanthoid Verbenaceae with bordered pits on the imperforate tracheary elements of the secondary xylem, a feature found in all Chloanthoideae. One can speculate that *Tectona* arose following the dispersal of an Australian physopsid ancestor to an environment in the Malay Archipelago that was conducive to the evolution of an arborescent habit. The range of *Tectona* currently comes within about 500 miles of that of the Physopsideae.

Since ten of the OTUs in Group C are exemplar species of the paraphyletic genus *Pityrodia*, the relationships hypothesized within the group might have been quite different if the other 31 species of *Pityrodia* had been included as well. Furthermore, there are additional characters (e.g., leaf morphology) that were excluded because of excessive intra-OTU variation in other parts of the study group but that would be useful in an analysis restricted to Group C. Consequently, the relationships shown within the Chloanthoideae (the upper two-thirds of Group C) are presented with relatively little confidence. For example, *Chloanthes* would probably have grouped with *Pityrodia uncinata* rather than *P. angustisepala* if more leaf characters had been included in the data set. On the other hand, the relationship hypothesized here between *Hemiphora* and *Pityrodia bartlingii* is well supported by shared foliar features that were not used in this analysis. The similar and unusual pollen morphology exhibited by these two taxa has already been noted by Raj & Grafström (1984).

AFFINITIES OF PHYSOPSIS AND FARADAYA

Although the groupings in Figure 1 are markedly incongruent with the accepted taxonomy of the Verbenaceae, they make intuitive sense if one is willing to look beyond the single-character taxonomy that underlies our current classification and consider the range of characters used here. However, the validity of one grouping (marked with an asterisk in Fig. 2) must be questioned. Its five genera belong to five different tribes in three subfamilies. The synapomorphies of this ostensible clade and the slightly larger one that includes *Neorapinia* are actinomorphic flowers, a corolla with four similar petals, a calyx with four similar sepals, and

stamens of equal length. Although these characters are not obligately correlated with each other in the data set as a whole (and therefore all of them have been retained in the analysis), neither can they be viewed as fully independent. Not only does the definition of actinomorphy overlap the other three characters, but the tetramerous construction of the corolla and calyx is very likely genetically linked. Thus the four characters that delimit this group would perhaps better be viewed as constituting only a single derived floral syndrome. While the true affinities of *Callicarpa*, *Hymenopyramus*, and *Petitia* remain obscure, *Physopsis* and *Faradaya* are probably not related to them.

In my opinion, a more plausible position for *Physopsis* is its traditional placement within tribe Physopsideae (perhaps close to *Mallophora* and *Dicrastylis* in Fig. 4), although it lengthens the tree by one step. Derived states that support this hypothesis include an indumentum of branched trichomes and the persistence of the corolla as a sheath around the fruit. Similarities in habit and foliar features that were not included in the analysis provide further support for a close relationship between *Physopsis* and the other Physopsideae.

The true affinities of *Faradaya* most likely lie within group B, where it may be closely related to *Oxera* (lower part of Fig. 3). This hypothesis is only one step longer than the most parsimonious trees. Like most members of group B, *Faradaya* has spinulose pollen; indeed, it is the only genus outside of group B that exhibits this derived state. Another unusual feature (character 56), found only in *Faradaya*, *Oxera*, *Hosea*, and a few species of *Clerodendrum* (all except *Faradaya* in group B), is the marked elongation of the ovary lobes relative to the unlobed portion of the ovary during fruit maturation. The exine of *Faradaya* has not yet been examined with transmission electron microscopy; if it proves to have branched columellae, a position in group B will be further supported, whereas simple columellae would argue against this hypothesis.

TAXONOMIC IMPLICATIONS

If future work supports the preliminary results presented here, some realignments in the classification of the Labiatae and Verbenaceae will be in order. The relationships shown in Figure 1 present two basic problems: polyphyly of the Labiatae and paraphyly of the Verbenaceae. The former could be remedied by restricting the family to the clade that includes the gynobasic-styled Labiatae, tribe Scutellarieae, the six genera of tribe Ajugeae that

have suprareticulate pollen, and two genera currently placed in the Verbenaceae: *Garrettia* and *Holmskioldia*. The remaining 13 genera currently assigned to the Labiatae by some or all authors (viz., tribe Prostanthereae, *Amethystea*, *Rubiteucris*, *Schnabelia*, *Tetraclea*, *Teucrium*, and *Trichostema*) would be transferred to the Verbenaceae, which would, however, remain paraphyletic. An alternative approach that would remedy this problem as well would be the adoption of Junell's (1934) proposal that the Verbenaceae be restricted to subfamily Verbenoideae and that most other groups of Verbenaceae sensu lato (including all ingroup genera in this analysis) be transferred to the Labiatae. Synapomorphies can be hypothesized for both families if delimited in this way. These two approaches to the classification of the Lamiales are considered in more detail elsewhere (Cantino, 1992).

Regardless whether one recircumscribes the Verbenaceae and Labiatae as suggested above or retains the conventional family boundary, it is clear that the current taxonomy of the Verbenaceae provides a very poor reflection of phylogenetic relationships. If the relationships shown in Figure 1 are essentially correct, subfamily Caryopteridoideae and tribes Callicarpeae, Chloantheae, Clerodendreae, Physopsideae, and Tectoneae are all polyphyletic while the Viticeae are paraphyletic. Only Monochileae emerge as a clade. At the generic level, *Pityrodia* and *Clerodendrum* are at best paraphyletic, and *Caryopteris* appears to be polyphyletic. If the slightly less parsimonious placements of *Physopsis* and *Faradaya* (discussed above) are correct, Physopsideae would no longer be polyphyletic, but the other problems would remain unchanged.

Infrafamilial groupings in the Labiatae hold up far better, in spite of the polyphyly of the family as a whole. Tribe Prostanthereae, Subfamily Nepetoideae sensu Erdtman (1945), and subfamilies Scutellarioideae and Lamioideae sensu Wunderlich (1967) emerge as monophyletic, the lattermost represented here by *Galeopsis*, *Lamium*, *Moluccella*, *Physostegia*, and *Prasium* (Fig. 2). Tribe Ajugeae, however, is polyphyletic. The implications of this analysis with regard to infrafamilial classification of the Labiatae are discussed in more detail elsewhere (Cantino, 1992).

BIOGEOGRAPHIC IMPLICATIONS

The gynobasic-styled Labiatae, which emerge as a clade in the strict consensus tree (Fig. 1), make up about 90% of the family. The distributions of their closest relatives suggest that this large and

successful clade originated in southern China or Indomalaysia, as suggested by Wu & Li (1982). *Holocheila* is known only from southern China (Yunnan Province), while *Acrymia, Cymaria,* and *Garrettia* are endemic to southeast Asia and/or Indomalaysia. *Ajuga* is widespread in the Old World but particularly diverse in China.

Two groups of Labiatae appear to have originated in Australia—tribe Prostanthereae and *Teucrium.* The former observation is trivial since the Prostanthereae are endemic to Australia, but an Australian origin for *Teucrium* runs counter to expectations, inasmuch as its center of diversity is in the Mediterranean region. The closest relatives of *Teucrium* (Figs. 1, 3) are *Teucridium, Spartothamnella,* and *Oncinocalyx,* the former endemic to New Zealand and the latter two to Australia. While *Teucrium* clearly experienced a major radiation in the Mediterranean region, there is no reason to assume it was the primary radiation rather than a secondary burst of evolution some time after the genus came into existence in another part of the world. In this regard, an argument can be made that the most primitive portion of the genus is section *Teucrium.* The rest of the genus is united by a derived calyx morphology: a bilaterally symmetrical and more or less gibbous calyx with an oblique attachment of the pedicel (Kästner, 1978; Cantino, unpublished data). In contrast, the calyx in section *Teucrium* is radially symmetrical with a central pedicel attachment, very similar to the calyx morphology in *Teucridium, Spartothamnella,* and most members of the *Trichostema–Caryopteris* alliance. If one accepts the basal position of section *Teucrium,* an Australian origin for the genus is no longer improbable. Section *Teucrium* is widespread in the Southern Hemisphere, including Australia and southern Africa, but also occurs in the Mediterranean region. It is suggested here that the current diversity of the genus resulted from a secondary radiation following the arrival of section *Teucrium* in the Mediterranean region, perhaps via Africa. A cladistic analysis of relationships within *Teucrium,* utilizing a wider range of characters, would provide a test of this hypothesis.

FURTHER RESEARCH

This analysis is preliminary in several important ways. First, the existence of a large number of equally parsimonious trees, with the resulting poor resolution of the strict consensus tree, may in part be due to the extent of missing data for certain characters and taxa. An effort is in progress to fill many gaps in the data matrix. Second, a future analysis will benefit from the inclusion of the segregate families Avicenniaceae and Symphoremataceae, as well as a more extensive sample of the gynobasic-styled Labiatae. Most important, the primary outgroups (Verbenoideae, Cyclocheilaceae, Nesogenaceae, Phrymaceae, and Stilbaceae) will be included in the data set of a subsequent analysis once data collection is complete, thereby eliminating the need for Lundberg Rooting. If relationships within the Scrophulariales–Lamiales clade can be better resolved, the most closely related groups of Scrophulariales should also be included as secondary outgroups.

This study provides a set of explicit hypotheses about relationships in the Lamiales. These will be tested by means of the improved analysis discussed above and through molecular–phylogenetic studies that have recently been initiated by R. G. Olmstead (pers. comm.). It is hoped that this paper will stimulate phylogenetically oriented investigations using other sorts of characters as well (e.g., terpenoids). The consensus of all such studies should provide a greatly improved understanding of the phylogeny of the Lamiales and a more natural and predictive classification of the Verbenaceae and Labiatae.

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PHYLOGENY OF THE RUBIACEAE (CHIOCOCCEAE) BASED ON MOLECULAR AND MORPHOLOGICAL DATA— USEFUL APPROACHES FOR CLASSIFICATION AND COMPARATIVE ECOLOGY[1]

Birgitta Bremer[2]

ABSTRACT

Phylogenies reconstructed with molecular data may provide new hypotheses of relationships. These may serve as a basis for improved morphological analyses and comparative analyses of ecological features. In this study a new phylogenetic hypothesis based on a chloroplast DNA restriction site analysis of the Rubiaceae prompted a critical analysis of morphological characters. Several unique morphological characters were identified that support a large, previously unrecognized monophyletic group, including the tribe Chiococceae. Hence, the tribe Chiococceae is amended to include members of the former Condamineeae (subtribe Portlandiinae) and the genera *Exostema* and *Coutarea* (formerly in the Cinchoneae). The new phylogeny of the Rubiaceae, based on molecular data and the great variety of fruits in the family, makes this family suitable for comparative studies of evolution of dispersal systems and for testing hypotheses of species diversity in connection with the different dispersal systems. In the Rubiaceae, fleshy fruits, adapted to animal dispersal, have originated a limited number of times and have remained unchanged since the time of origin. The hypothesis that animal dispersal should promote species diversity is not supported for the Rubiaceae.

The position of the Rubiaceae in the order Gentianales close to the Loganiaceae was first suggested by Utzschneider (1947) and later established by Wagenitz (1959, 1964). This systematic position is accepted by most systematists dealing with higher-level classification (Dahlgren, 1980; Thorne, 1983; Takhtajan, 1987) and also is supported by phytochemistry (cf. Bisset, 1980) and sequence data of the *rbc*L gene (R. Olmstead & J. Palmer, pers. comm.). Relationships within the order are unresolved and have been proposed to be reticulate (Leeuwenberg & Leenhouts, 1980), with the Loganiaceae as a central or "ancestral" paraphyletic taxon. A morphological study, aimed at identifying the sister group to the Rubiaceae, analyzed representatives of all tribes of the Loganiaceae as well as a few taxa of the other families of the Gentianales (Bremer & Struwe, unpublished data). The results confirmed that the Loganiaceae were paraphyletic. The closest relatives to the Rubiaceae were found to be a part of the Loganiaceae, *viz* the tribe Gelsemieae or at least a part of it.

The Rubiaceae are, with the exception of a few aberrant taxa, an easily circumscribed family, characterized by inferior ovary, opposite leaves with stipules, and absence of internal phloem. Intrafamilial delimitations have always been complicated and uncertain, however. There are two main reasons for this uncertainty. First, "traditional" classification is based on phenetic similarities, and hence several groups are defined by symplesiomorphies or mere absences of characters. Second, much emphasis has been put on fruit structures for sorting genera into subfamilies and tribes. Single structures have been used as cardinal characters. However, in this family comprising about 10,000 species and 600 genera (Mabberley, 1987), many different fruit traits occur. If evolutionary shifts in these traits are common, i.e., highly homoplastic, they may be a source of error in classification. During the past 35 years three important treatments of the family with new classification schemes have been presented (Verdcourt, 1958; Bremekamp, 1966; Robbrecht, 1988). A comparison of these

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different schemes (Bremer & Jansen, 1991, table 2) displays many dissimilarities and conflicts, even though there is also much congruency. The merits of the different systems are difficult to evaluate because, in several cases, they are based on a few cardinal characters only, and no strict character analyses are presented. So far, studies of relationships between the subfamilial entities have been rare. Affinities between high-level Rubiaceae taxa have been addressed by serological similarities (Lee & Fairbrothers, 1978). The first phylogenetic analysis of representatives of different tribes of the family is the one by Bremer & Jansen (1991) based on chloroplast DNA (cpDNA) variation.

In order to evaluate different classification schemes, and to use the classification as a framework for evolutionary studies, phylogenetic analyses are necessary. In this context, neither molecular nor morphological data are superior. Both types of data are useful for phylogenetic reconstruction. When a phylogeny based on molecular data is compared with an "accepted" classification, the latter is often rejected because most classifications today are based on phenetic similarity and do not reflect the phylogeny (cf. Sytsma, 1990). However, this does not mean that morphological data should be dismissed as inferior for phylogenetic reconstruction. With cladistic analysis, both molecular and morphological data may be useful and complementary in phylogenetic reconstruction. It is also important to get rid of preconceived notions concerning which characters are "good" or "useless." Character homoplasy and hence usefulness can only be determined a posteriori, following an analysis involving comparison with other characters.

Due to the correlation between large data sets (many taxa) and a high level of homoplasy (Sanderson & Donoghue, 1989; Archie, 1989), it is probably not realistic to expect to resolve all relationships in one analysis of all genera of a large family such as the Rubiaceae. However, if not all taxa are analyzed, character optimization and tree topology may be affected (Donoghue et al., 1989). In Rubiaceae it is not sufficient to sample only a few examples of each tribe in order to resolve tribal relationships, since the tribes in many cases are badly circumscribed (cf. Hallé, 1961; Steyermark & Kirkbride, 1975; Kirkbride, 1979; Ridsdale, 1982; Tirvengadum, 1984; Robbrecht & Puff, 1986; Bremer, 1987; Robbrecht, 1988). One strategy for tackling the sampling problem is to use "common knowledge" of relationships and select a limited number of taxa for a pilot study with molecular data. Results of a pilot study may suggest

new hypotheses of relationships, as in the study by Bremer & Jansen (1991). In that study, a cladistic analysis of cpDNA restriction data was performed for 33 genera representing 18 tribes and four subfamilies. Several monophyletic groups postulated in this analysis were congruent with "traditional" classification, e.g., the subfamilies Rubioideae and the Ixoroideae. However, the large subfamily Cinchonoideae was shown to be paraphyletic. In addition, totally new relationships were indicated.

Following such a molecular pilot study, the postulated new relationships may then be tested by morphological data. If the new groupings are supported, it should be possible to identify larger monophyletic groups defined by particular morphological characters. This morphological study may subsequently suggest suitable taxa for new molecular and morphological analyses that may provide further support for particular intrafamilial taxa. Using a sample of representatives from these larger corroborated monophyletic taxa, it should be possible to analyze and reconstruct the phylogeny and resolve the relationships for the whole family. This is an enormous task for the Rubiaceae, but important for a stable and informative classification.

The first steps in the strategy outlined above are here illustrated by an example in which a new relationship indicated by a cpDNA analysis (Bremer & Jansen, 1991) provides the basis for a morphological analysis, resulting in the identification of a large monophyletic group including the tribe Chiococceae, the subtribe Portlandiinae (of the Condamineeae) and some genera from other tribes.

Another kind of analysis that can be performed is comparative study of ecologically important characters. Such an analysis is founded on the assumption that phylogenetic reconstruction provides information on evolutionary sequences. The usefulness of a phylogenetic reconstruction based on molecular data for testing ecological characters or hypotheses will be illustrated and discussed.

A CASE STUDY—CHIOCOCCEAE

The cpDNA cladogram of the Rubiaceae (Bremer & Jansen, 1991, fig. 2) revealed several hitherto unknown relationships. One of the branches in the cladogram (Bremer & Jansen, 1991, fig. 2) included four genera, *Exostema* and *Coutarea* of the tribe Cinchoneae and *Erithalis* and *Chioccocca* of the Chiococceae. The members of the tribe Chiococceae (*Chioccocca*, Fig. 1) have many small flowers in axillary inflorescences, mostly fleshy fruits (drupes), and one seed per carpel, whereas *Exo-*